A NEW GENUS OF HENICOPID CENTIPEDE (CHILOPODA: LITHOBIOMORPHA) FROM NEW CALEDONIA

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Two species from New Caledonia, *Easonobius tridentatus* gen. et sp. nov. and *Paralamyctes humilis* Ribaut, 1923, together represent a new genus of Henicopini. South African species formerly classified together with *Easonobius humilus* in *Analamyctes* Chamberlin, 1955, are distantly allied, members of *Paralamyctes* (*Paralamyctes*) Pocock, 1901. Morphological characters of *Easonobius*, including electron microscopic study of the head, indicate membership in the *Lamyctes-Henicops* Group. Parsimony analysis favours a closest relationship between *Easonobius* and the Australasian genus *Henicops* Newport, 1844. The type species of *Lamyctes* (*Eumyctes*) Chamberlin, 1951, shares apomorphie characters with the Cape genus *Lamyctopristus* Attems, 1928, to which *Eumyctes* is transferred. □ *Chilopoda, Lithobiomorpha, Henicopidae,* Easonobius, *New Caledonia, taxonomy, phylogeny.*

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Paralamyctes humilis Ribaut, 1923, was named based on a single, small male from Oubatche in northeastern New Caledonia. Subsequently, Chamberlin (1955) reassigned *P. humilis* to the genus *Analamyctes* Chamberlin, 1955, and, more precisely, to an invalidly erected subgenus *Capolamyctes*. *Analamyctes* (*Analamyctes*) was conceived as occurring in Argentina (the type species *A. tucumanus* Chamberlin, 1955, from Tucumán Province, and *Paralamyctes andinus* Silvestri, 1903, from Mendoza Province). *Analamyctes* (*Capolamyctes*) received species from the Cape region of South Africa (*Paralamyctes aspernlus* Silvestri, 1903; *P. levigatus* Attems, 1928; *P. tabulinus* Attems, 1928) together with the New Caledonian *P. humilis*.

In a revision of *Paralamyctes* Pocock, 1901, Edgecombe (2001) dismissed Chamberlin's (1955) reassignment of South African species to *Analamyctes*, these taxa being accommodated within a monophyletic *Paralamyctes* (*Paralamyctes*) Pocock, 1901. This conclusion is supported by both morphological (Edgecombe, 2003a) and molecular data (Edgecombe & Giribet, 2003a). A reconsideration of *Analamyctes* was made possible by a restudy of its type species, *A. tucumanus*. Argentinian species of *Analamyctes* are members of a *Lamyctes-Henicops* Group, only distantly allied to *P.* (*Paralamyctes*) (Edgecombe, 2003b).

The present study reconsiders *Paralamyctes humilis*, which until now has defied phylogenetic

placement. New collections made by G. B. Monteith (Queensland Museum) in New Caledonia include additional specimens of both sexes of this species, as well as specimens that represent another, closely related species. Morphology of these species is documented by electron microscopy, including mouthparts that have proven useful in henicopid systematics, and they are are coded for their morphological characters in a dataset for henicopid phylogeny.

Institutional abbreviations cited in this work are: AM – Australian Museum, Sydney; MNHN – Museum National d'Histoire Naturelle, Paris; QM – Queensland Museum, Brisbane; ZMB – Museum für Naturkunde, Berlin. Morphological terminology is as explained by Edgecombe (2001: 203). Drawings were prepared with a camera lucida attachment to a Leica MZ12. Scanning electron microscopy used a Leo 435VP with a Robinson backscatter detector, and digital images assembled into plates with Photoshop.

SYSTEMATICS

Easonobius gen. nov.

partim *Analamyctes* (*Capolamyctes*) Chamberlin, 1955 nomen nudum.

TYPE SPECIES. *Easonobius tridentatus* gen. et sp. nov.

ETYMOLOGY. In honour of Dr Edward H. Eason (1915-1999), for his contributions to lithobiomorph systematics, with the standard suffix, -obius.

DIAGNOSIS. Member of *Lamyctes-Henicops* Group lacking pseudoporodont (shared with

Henicops and *Analamyctes*); posterior angles of tergites 7, 9, 11 and 13 produced (shared with *Henicops* and *Lamyctopristus*); dental margin of maxillipede coxosternite with 2+2 or 3+3 teeth; tarsi of all legs bipartite (shared with *Analamyctes*); coxal process of first maxilla with laciniate or plumose setae near dorsal margin (shared with *Henicops*); mandible with single row of exclusively bipinnulate aciculae; last distal spinose projection on tibia of leg 13; first genital sternite of ♂ undivided (plesiomorphies excluding membership in *Henicops*). Antenna with 26-33 articles; tergite of intermediate segment with strongly concave posterior margin.

ASSIGNED SPECIES. *Paralamyctes humilis* Ribaut, 1923.

DISCUSSION. Chamberlin distinguished two subgenera of *Analamyctes* in a key, using a single character. *Analamyctes* (*Analamyctes*), grouping the Argentinian species *A. tucumanus* and *A. andinus*, was defined based on 'posterior angles of none of the dorsal plates produced'. *Analamyctes* (*Capolamyctes*) grouped *A. humilis* with three nominal South African species of *Paralamyctes* (Edgecombe, 2001, 2003a). *Analamyctes* (*Capolamyctes*) was distinguished based on 'posterior angles of tergites 9, 11 and 13 or 7, 9, 11 and 13 produced'. Though Chamberlin was explicit about the membership and diagnosis of *Capolamyctes*, he neglected to designate a type species. The name fails Article 13.3 of the ICZN Code, and is dismissed as a *nomen nudum*. As argued in detail below, the original concept of *Capolamyctes* delimits a polyphyletic group. Of Chamberlin's assigned species, only *Paralamyctes humilis* is at all closely related to the type species of *Analamyctes*.

Easonobius resembles *Analamyctes* in having bipartite tarsi on all legs, a state restricted to these taxa within the *Lamyctes-Henicops* Group (but possibly plesiomorphic by comparison to *Paralamyctes* and Zygethobiini). *Easonobius* most obviously differs from *Analamyctes* in its tergal shapes, as used in Chamberlin's (1955) subgeneric scheme, with projections on TT7, 9, 11 and 13 versus nearly transverse margins in *Analamyctes*. This does not in itself obviate a close relationship, since tergite projections occasionally vary within some well defined henicopine clades, such as *Paralamyctes* (*Haasiella*), e.g., present in *P.* (*H.*) *subicolus* and *P.* (*H.*) *trailli*; absent in *P.* (*H.*) *cammooensis* and *P.* (*H.*) *ginini*.

Easonobius is resolved as most closely related to *Henicops* Newport, 1844, in the best supported phylogenetic analyses, described below. However, several apomorphic characters unite Australian and New Zealand members of *Henicops* in the traditional sense (e.g., Attems, 1914, 1928; Chamberlin, 1920; Archey, 1937) as a clade that excludes *Easonobius*. These characters (numbered as in Table 1) include a subdivision of the basitarsus indicated by paired larger setae (40:1), the first genital sternite of the ♂ being divided longitudinally into two sclerites (43:1), the distitarsus of leg 15 being divided into tarsomeres (53:1), and more setose gonopods in both sexes. *Henicops* as traditionally delimited is strongly supported (jackknife frequency 99%; Fig. 8), and it is not expanded in scope and rediagnosed to incorporate the species here recognised as *Easonobius*.

Comparable in several respects is a group of mostly Southern African species referred to *Lamyctes* (*Eumyctes*) Chamberlin, 1951 [type *Henicops sinuatus* Porat, 1893] and *L.* (*Neomyctes*) Chamberlin, 1951 [type *Lamyctes* (*Neomyctes*) *ergus* Chamberlin, 1951]. These are distinguished from typical *Lamyctes* Meinert, 1868, by their projections on tergites 9, 11 and 13. The style of tergite projections in species such as *L.* (*Eumyctes*) *sinuatus* is as in *Easonobius*, and these species also share a strongly concave posterior margin to the tergite of the intermediate segment (Attems, 1909, fig. 53). Chamberlin's (1951 versus 1955) distinction between *Eumyctes*/*Neomyctes* and *Analamyctes* (including *E. humilus*) placed fundamental weight on the absence or presence of a tarsal articulation. A closer relationship can be proposed for the type of *Eumyctes*, *L.* (*E.*) *sinuatus*, and the Cape genus *Lamyctopristus* Attems, 1928, than the former shares with *Easonobius*. *Lamyctes* (*Eumyctes*) *sinuatus* has dense, strongly developed tuberculation on the tergites, to a degree observed only in *Lamyctopristus* amongst all known Henicopidae. In both *L.* (*E.*) *sinuatus* and *L. granulosus* (=*L. validus?*), tuberculation is more pronounced on the male than on the female (Lawrence, 1955: 23), e.g., being well developed on the head shield of the male. These species are also similar, and resemble *Henicops* Newport, 1844, in having tergite projections and distal spinose projections on the tibia of leg 14. They share other peculiar characters in addition to their tergal tuberculation. In *Lamyctopristus validus* as well as *Lamyctes* (*Eumyctes*) *sinuatus*, the tarsi of
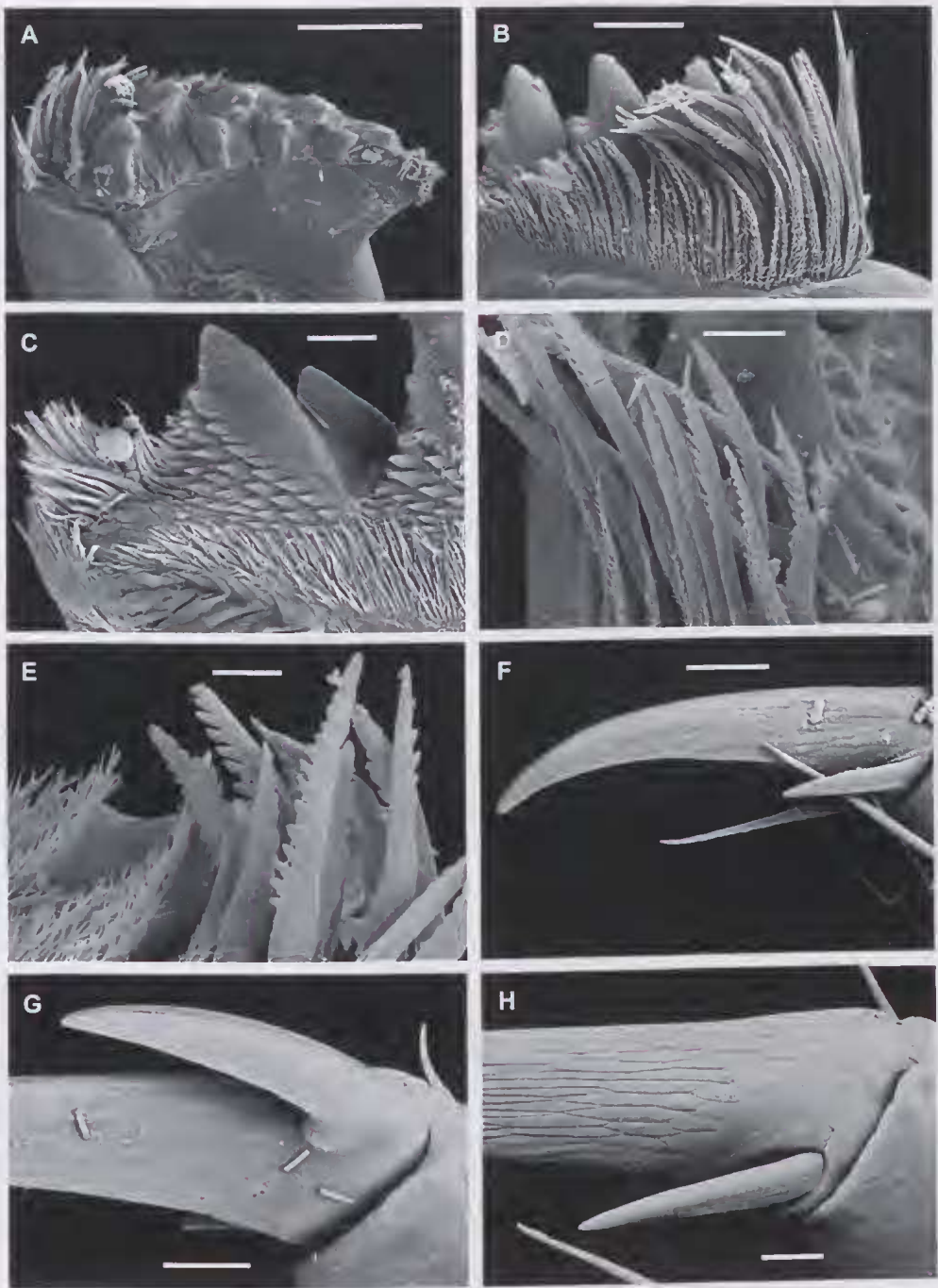
FIG. 1. A-F, *Lamyctopristus* (*Eumyctes*) *sinuatus* (Porat, 1893). ZMB 4962, ♀, Kamaggas, Northern Cape Province, South Africa. A-E, mandible. A, medial view of gnathal edge, scale 100μm; B, ventral part of gnathal edge, scale 50μm; C, dorsalmost tooth and furry pad, scale 20μm; D-E, aciculae, scales 20μm, 10μm; F, anterior view of pretarsus, scale 30μm. G, *Henicops maculatus* Newport, 1844. Anterior view of pretarsus of leg 14, scale 15μm. H, *Paralamyctes* (*Paralamyctes*) *asperulus* Silvestri, 1903. SAM-ENW-C5314. Anterior view of pretarsus of leg 14, scale 15μm.
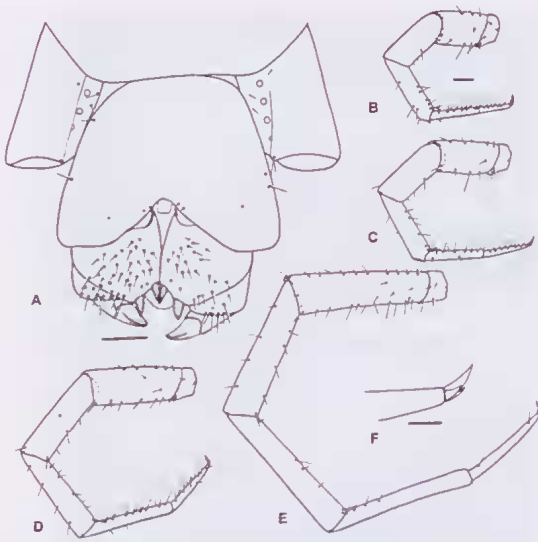
FIG. 2. A, *Lamyctopristus* (*Eumyctes*) *sinuatus* (Porat, 1893). ZMB 4962, ♀, Kamaggas, Northern Cape Province, South Africa, terminal segments and gonopods, scale 200µm. B-F, *Easonobius tridentatus* gen. et sp. nov. QM S60291, ♀, Pie d'Amoa. Scale in B applies to C-E. B, leg 12, scale 200µm; C, leg 13; D, leg 14; E, leg 15; F, distal part of tarsus and pretarsus of leg 15, scale 100µm.

anterior legs have a distinct curvature within the distitarsal portion, this occurring despite the lack of articulations. Mandibular characters (Fig. 1) are also consistent with a close relationship between *L.* (*Eumyctes*) *sinuatus*, *Lamyctopristus* and *Henicops*. The former species has a large number of aciculae on the mandible, with the density and arrangement of the aciculae two-deep (Fig. 1B, D), rather than a single row, being otherwise observed only in *Lamyctopristus validus* (Edgecombe, 2003b, fig. 34D) and in all species of *Henicops* (Edgecombe et al., 2002, fig. 5C). Also as in *Henicops* and *Easonobius*, but not *Lamyctes*, the accessory denticles on the dorsalmost tooth of the mandible arc simple, angular elements (Fig. 1C), rather than multifurcating scales (Edgecombe et al., 2002, fig. 7B, for *Lamyctes emarginatus*). As well, the novel expansion of basal article of the female gonopod in *Lamyctopristus* may have a precursor in the relative breadth of this article in *L.* (*E.*) *sinuatus* (Fig. 2A). Phylogenetic analysis including these characters (see below) recognises *L.* (*Eumyctes*) *sinuatus* as more closely related to *Lamyctopristus* than to *Lamyctes*. To incorporate this relationship into the classification, *Eumyctes* is reassigned to *Lamyctopristus*.
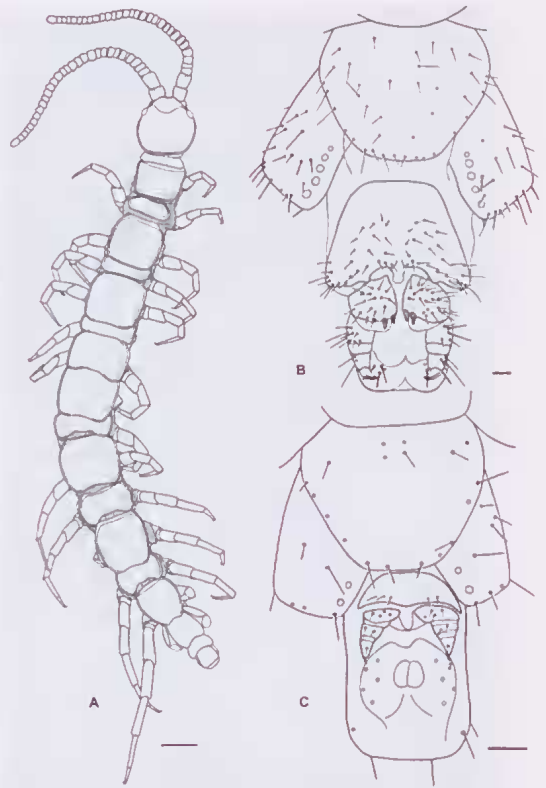

FIG. 3. *Easonobius tridentatus* gen. et sp. nov. A, MNHN P244, holotype ♀, Pie d'Amoa, dorsal habitus, scale 1mm; B, QM S60291, ♀, Pie d'Amoa, terminal segments and gonopods, scale 100µm. C, QM S60292, ♂, Aoupinie, terminal segments and gonopods, scale 100µm.

Easonobius tridentatus sp. nov.
(Figs 3-6)

DIAGNOSIS. *Easonobius* with width of head shield up to 1.5mm; penultimate and preceding few antennal articles as wide as or wider than long; dental margin of maxillipede coxosternite moderately wide, gently convex, with 3+3 teeth; Tömösváry organ small; a few lacinate setae on coxal process of first maxilla; posteromedian embayment in margin of T7 transverse or faintly convex; short, spinule-like setae on tergites and along tergal margins.

ETYMOLOGY. For the three teeth on the dental margin of the maxillipede coxosternite.

MATERIAL. HOLOTYPE. MNHN P244, ♀ (Fig. 3A), Pie d'Amoa, N slopes, Province Nord, New Caledonia, 20°58'S 165°17'E, 500m, G.B. Monteith, 24 November 2001-31 January 2002. PARATYPES. QM S60291, ♀
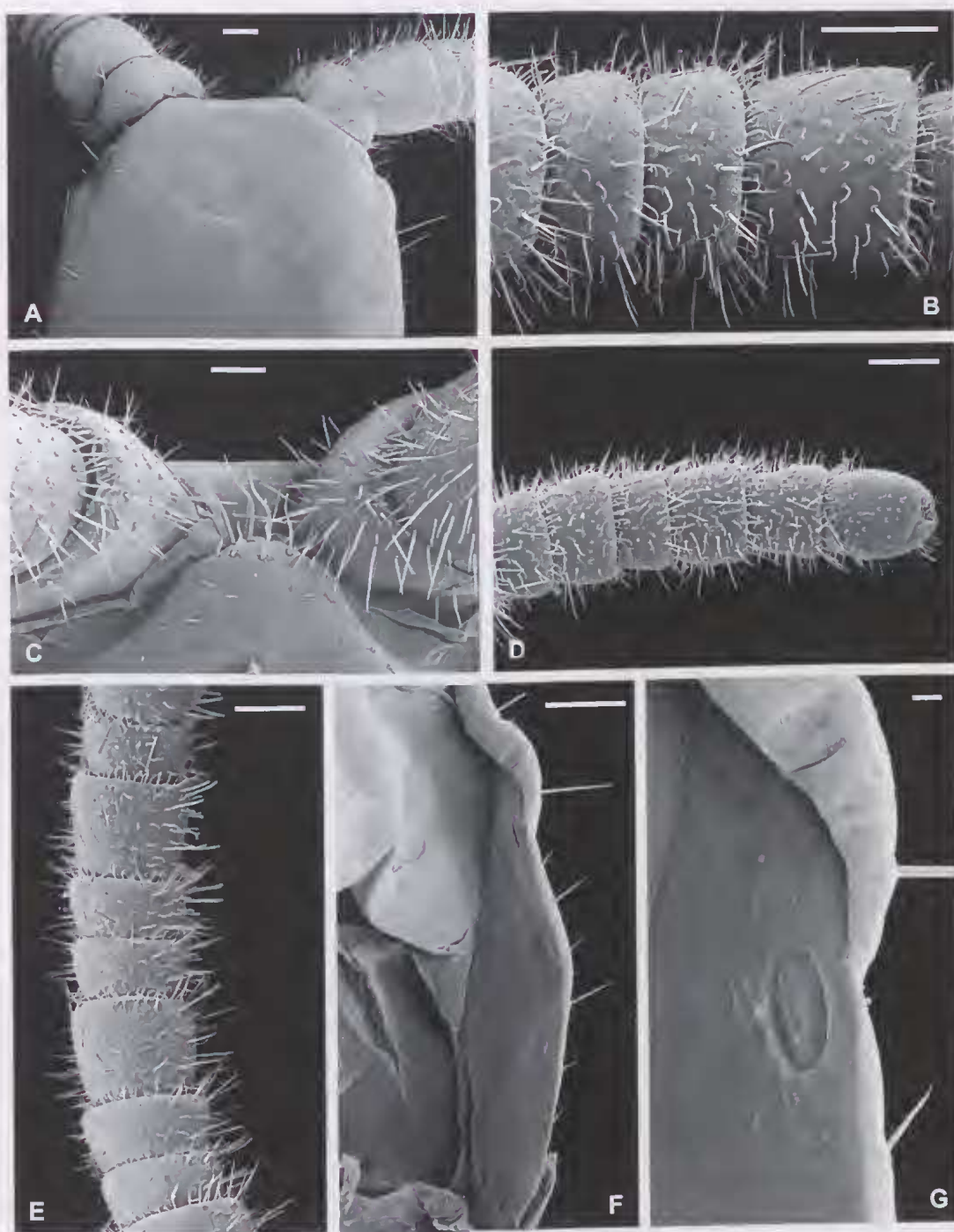
FIG. 4. *Easonobius tridentatus* gen. et sp. nov. SEMs, scales 100μm except G, 10μm. QM S60291, ♀, Pic d'Amoa. A, dorsal view of anterior part of head, proximal part of antennae; B,D,E, dorsal side of antenna; C, ventral view of clypeus and sclerotised bridge between antennae; F-G, cephalic pleurite and detail of Tömösváry organ.
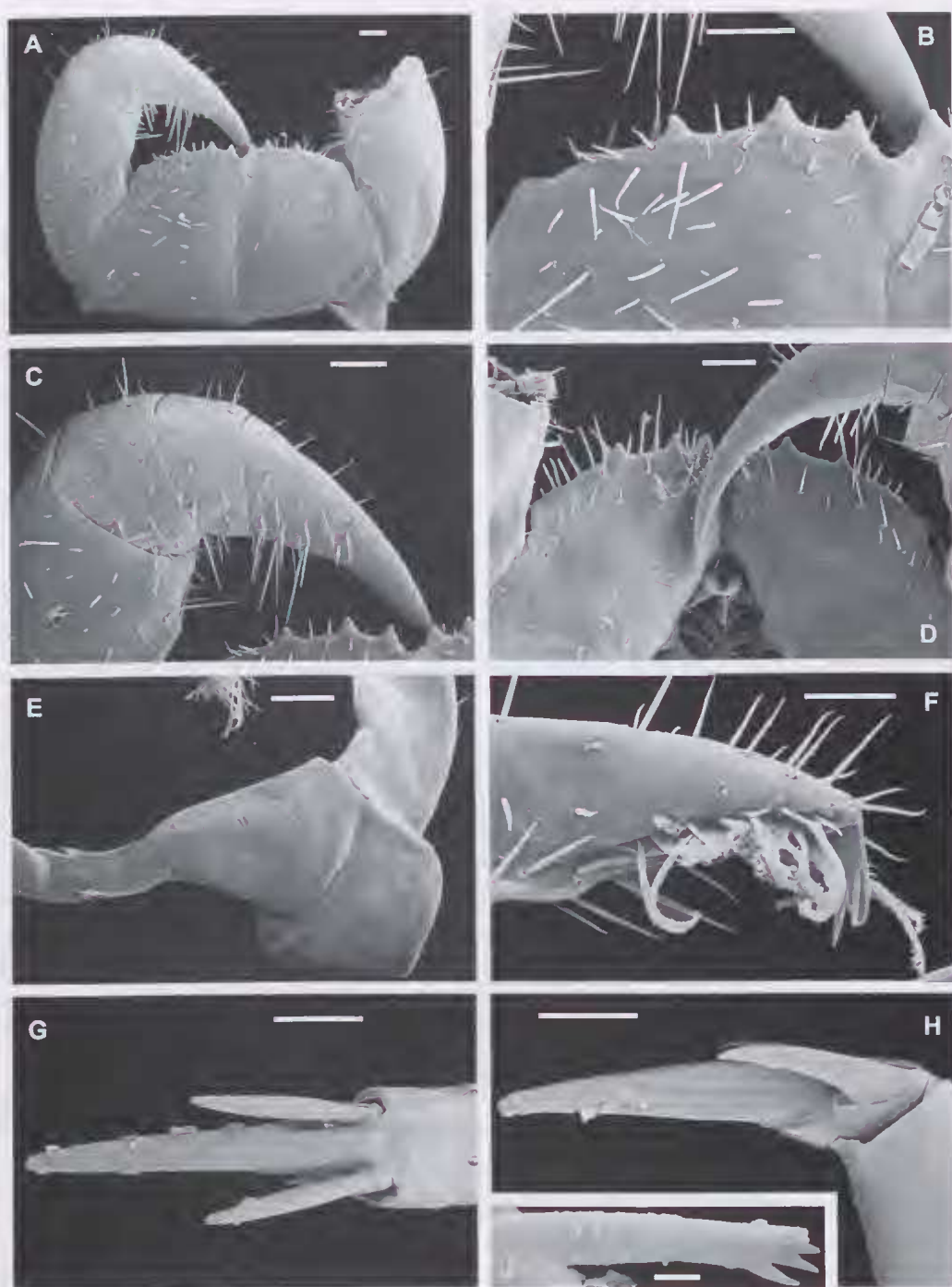
FIG. 5. *Easonobius tridentatus* gen. et sp. nov. SEMs, scales 100μm except F, 50μm, G-H, 20μm, I, 2μm. A-F, I, QM S60291, ♀, Pic d'Amoa. A, ventral view of maxillipede; B, detail of dental margin of coxosternite; C, maxillipede telopodite; D, dorsal view of coxosternite; E, second maxilla; F, tarsus and claw of second maxilla; I, distal part of lacinate seta on coxal process of first maxilla. G-H, AM KS 81365, ♀, Pic d'Amoa, dorsal and posterior views of claw, accessory claws and sensory spur of leg 14.

(Figs 2B-F, 3B, 4, 5A-F, I, 6), AM KS 81365. ♀ (Fig. 5G-H), from type locality, G.B. Monteith, 31 January 2002. OTHER MATERIAL. New Caledonia, leg. G.B. Monteith. PROVINCE NORD: QM S60292, ♂ (Fig. 3C), 21°11'S 165°18'E, Aoupinie, top camp, 850m, 2-4 November 2001. PROVINCE SUD: QM S60293, ♂, 21°45'S 166°00'E, Mt Do summit, 1000m, 21 November 2000.

DESCRIPTION. Length (head shield to end of telson, slightly extended specimen) up to 16mm; width of head shield up to 1.5mm. Colour (based on specimens in absolute ethanol): head shield orange with purple mottling, including region surrounding ocellus; antenna pale orange, sometimes with pale lavender tint along most of length; tergites lavender with deep purple longitudinal median band and mottling beside/on borders; sternites pale lavender except for orange sternites 14 and 15; legs pale yellow except for pale yellowish-orange tarsi.

Head shield. Wider than T1-T5, equally wide as T7, with shallow median notch, lacking longitudinal median furrow (Fig. 4A); maximal posterior extent of transverse suture at about 26% length of head shield; border as wide medially as posterolaterally. Ocellus large, moderately domed (Fig. 4A). Tömösváry organ relatively small (Fig. 4G), with outer margin near edge of cephalic pleurite, beneath ocellus (Fig. 4F).

Clypeus with cluster of about six apical setae (anterior pair and transverse band of three or four), several smaller setae scattered posterolateral to these (Fig. 4C); usual band of four setae just in front of labrum. Labral margin gently concave where cluster of bristles projects beyond margin; numerous branches along length of each bristle.

Antenna. 34-38% length of body, 3.7 times length of head shield in largest specimen (Fig. 3A); 31-27 and 31-31 articles in ♀♀, 30-30 and 31-30 in ♂♂; basal two articles much enlarged relative to others (Fig. 3A); articles 3-4, 7-8, 10-11 and one or two more distal pairs short. Terminal article up to 2.2 times length of penultimate; most of distal articles of similar shape, slightly wider than long (Fig. 4D). Setal density similar from third article, with mix of longer trichoid sensilla and shorter curved sensilla (Fig. 4B, E); most setae oriented normal to antennal surface or sloping anteriorly, arranged in imprecisely defined whorls, as many as seven whorls on longer articles.

Maxillipede. Dental margin gently convex, with 3+3 teeth; outer tooth more distant than inner pair to each other (Fig. 5B), well inside anterolateral corner of dental margin. Median notch

moderately deep, parabolic or semicircular. Setae rather evenly scattered over anterior two-thirds of coxosternite (Fig. 5A); irregular band of short setae on anterior part of dorsal surface of coxosternite (Fig. 5D). Pretarsal part of tarsungulum about equal in length to tarsal part; long setae distinctly denser on inner side of tarsungulum than on outer (Fig. 5C); setation on tibia and femur fairly even on inner, outer and ventral sides.

Mandible. Four paired teeth (Fig. 6A). Eleven aciculae, each with large, blunt pinnules approximately symmetrical on anterior and posterior margins (Fig. 6C-D). Fringe of branching bristles skirts aciculae; ventral bristles with moderately wide bases, with even, rather dense branchings along entire length of each bristle (Fig. 6B); fairly abrupt transition to three overlapping rows of multifurcating scale-like bristles against second tooth; scales branch near their bases to form continuous fringe of slender, hair-like spines; fringe narrowing dorsally. Grooved ridges bearing row of blunt accessory denticles well developed on teeth (Fig. 6A-B); most accessory denticles small, triangular, even on dorsal tooth (Fig. 6E). Proximal part of dentate lamina consists of a narrow band of fused scales, strongly differentiated from furry pad (Fig. 6E); furry pad composed of simple and multifurcating bristles.

First maxilla. Coxal parts of coxosternum meeting along most of their length medially (Fig. 6F), separated posteriorly by small, wedge-shaped sternite. Coxal process with cluster of up to 15 simple setae at tip, a few setae along inner margin; four or five laciniate setae above simple setae near dorsal edge of coxal process (Fig. 6H), thicker than simple setae, branching into up to five short spines at their distal tips (Fig. 5I). Distal article of telopodite with two rows of up to 14 plumose setae along inner margin (Fig. 6G); plumose setal rows fringed along ventral side by row of shorter simple setae, along dorsal side on anterior half of article by row of slender spines, these more densely spaced than simple or plumose setae (Fig. 6G); ventral surface of distal article with numerous, evenly scattered simple setae.

Second maxilla. Sternite fused to coxa, margins distinct. Irregular band of about eight setae across anterior part of coxa (Fig. 5E). Joint between trochanter and prefemur defined as a notch along inner margin of telopodite (Fig. 5E). Inner face of tarsus with up to about 20 plumose setae, densely branching along their distal halves (Fig. 5F). Pretarsal claw small, composed of up to five
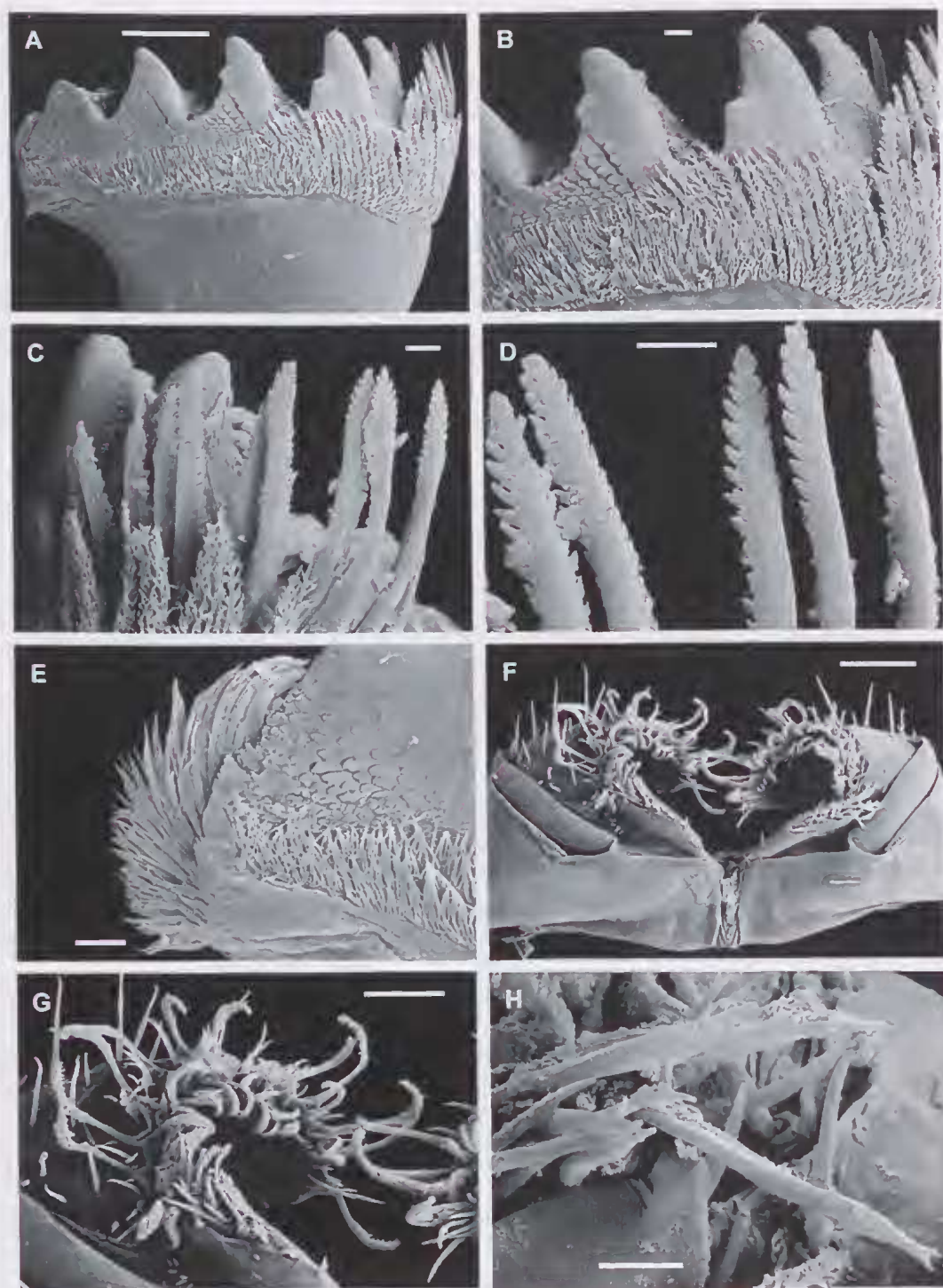
FIG. 6. *Easonobius tridentatus* gen. et sp. nov. SEMs. QM S60291, ♀, Pic d'Amoa. A-E, right mandible. A, gnathal lobe, scale 50μm; B, fringe of branching bristles and teeth, scale 10μm; C-D, aciculae, scales 10μm; E, furry pad, scale 10μm; F, first maxillae, scale 100μm; G, distal article of telopodite of first maxilla, scale 50μm; H, laciniate setae on coxal process of first maxilla, scale 10μm.

digits of varied length and thickness, median digit the largest (Fig. 5F).

Tergites (Fig. 3A).Weakly wrinkled, gently turned up against borders. T1 trapeziform, anterior width slightly less than T3, 81% width of widest tergite (T10), posterior margin transverse or faintly concave; posterior angles of TT1-5 rounded; lateral border subparallel in T3, posterior margin faintly or weakly concave; posterior margin of T5 distinctly concave, that of T8 slightly more so; TT9, 11 and 13 with strong, blunt projections and wide, transverse or convex median sector; T7 with shorter projections, median sector subtransverse or weakly convex; TT2, 4 and 6 bordered laterally, thickened posteromedially; TT10, 12 and especially 14 with concave posterior margins, blunt posterior angles. Tergite of intermediate segment with concave posterior margin in both sexes. Tergite of first genital segment less sclerotised than telson tergite. Short, spinule-like setae scattered across anterior third and laterally on long tergites; numerous short, spinule-like setae along lateral margins of tergites.

Legs. Distal spinose projection on tibiae of legs 1-13 (Fig. 2B, C), absent on 14 (Fig. 2D) and 15 (Fig. 2E). Legs 12-15 with length ratios 1: 1.2 : 1.6 : 2.5. Tarsal joints marked by desclerotised band and weak flexure on anterior legs, articulation weakly continuous on dorsal side of leg; distitarsus about 55% length of basitarsus on leg 12 (Fig. 2B), 63% length of basitarsus on leg 15; leg 15 basitarsus nine times longer than wide, distitarsus about 10 times longer than wide, tibia 5.5 times longer than wide (Fig. 2E). Prefemur with numerous short setae on dorsal and ventral sides, with one or a few longer setae near midlength on ventral side of legs 1-13; more evenly short setae on prefemur of legs 14-15; setae relatively fewer on femur and tibia, of similar size to most on prefemur, densest on tarsus; short setae on distitarsus of legs 1-14 sloping distally; setae relatively sparse on tibia and tarsus of leg 15. Anterior and posterior pretarsal accessory claws nearly symmetrical on all legs, about half length of main claw, weakly diverging (Fig. 5G); minute sensory spine on posterior side of claw base (Fig. 5H), lacking on anterior side.

Coxal pores. All round, separated by less than their diameter when abundant, inner pores smaller; 4,5,5,5/4,5,5,5 in largest ♀, 3,4,5,5/3,4,5,5 (Fig. 3B) and 2,3,4,4/2,3,4,4 in progressively smaller ♀♀; 3,3,4,3/3,3,3,3 in largest ♂, 1,2,2,2/1,2,2,2 in smaller ♂ (Fig. 3C);

pore row not set in a groove, separated from anteroventral face of coxa by rounded surface.

Female (Fig. 3B). Sternite of segment 15 weakly to gently convex posteromedially, fringed with short setae along posterior margin. Setae fairly evenly scattered on posterior two-thirds of sternite of first genital segment, few or lacking on anterior third; transverse band of setae slightly in advance of posterior margin. Gonopod with two relatively small, conical spurs, inner spur slightly smaller; up to 20 setae on basal article of gonopod, up to 8 on second article, two or three on distal article; claw simple.

Male (Fig. 3C). Sternite of segment 15 weakly convex posteromedially, most setae along margins. Sternite of first genital segment undivided, a few setae in front of posterior margin. Articles of gonopod with four, two, and one small setae (proximally to distally).

DISCUSSION. Specimens assigned to *Easonobius tridentatus* sp. nov. resemble *E. humilis* (Ribaut) in having a similar number of antennal articles (27-31 in the new species versus 26-33 in *E. humilis*), projections with the same shape on tergites 9, 11 and 13, a bipartite tarsus on legs 1-12, and absence of a pseudoporodont. The holotype of *Easonobius humilis* is a small male (width of head 0.75mm; length of body 6.6mm) lacking most legs, and no other material was assigned to the species by Ribaut (1923). The original illustrations are accurate except for the position of the Tömösváry organ, which was depicted as anterior to the ocellus (Ribaut, 1923, fig. 24) when in fact the organ lies beneath the ocellus in the holotype and in new specimens assigned to the species, as is also the case in *E. tridentatus*. Ribaut noted 33 antennal articles in the description based on the right antenna; the unfigured left antenna has 30 articles.

All specimens of *Easonobius tridentatus* are larger than specimens of *E. humilis*, and all have 3+3 teeth on the dental margin of the maxillipede (Fig. 5A-D) versus 2+2 teeth on a narrower margin in *E. humilis* (Fig. 7A-B). Although some henicopids have an ontogenetic increase in number of maxillipede teeth [*Paralamyctes validus*: Archey, 1921: 182; *Anopsobius neozelanicus*: Archey, 1937: 87; *Paralamyctes (Haasiella) cammooensis*: Edgecombe, 2003b], tooth numbers in the *Lamyctes-Henicops* Group are fixed early in ontogeny when the adult number is 2+2 or 3+3 teeth. For example, the dental formula 3+3 is complete by 8-legged larval stadium LII in *Henicops* from Victoria,
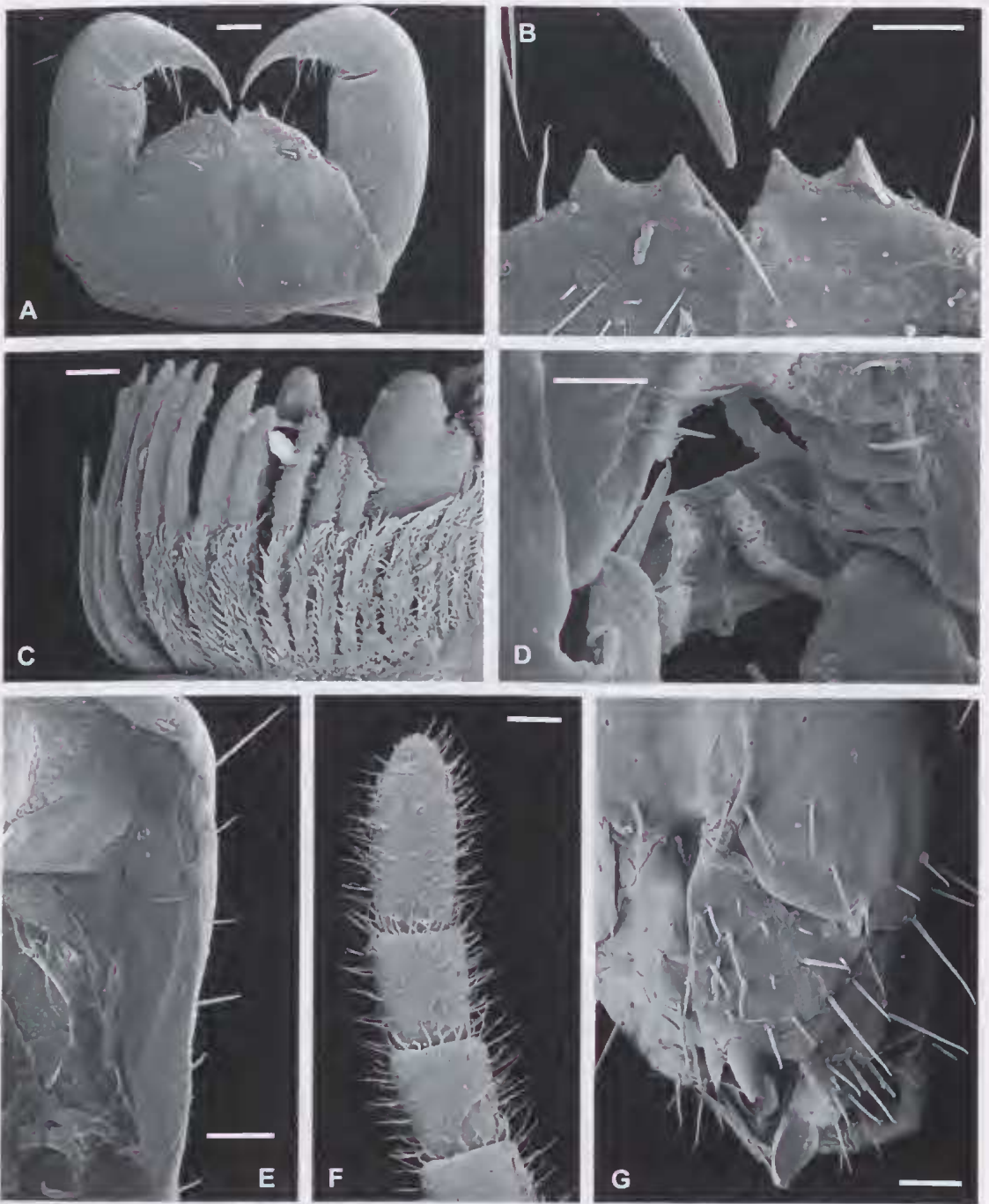
FIG. 7. *Easonobius humilis* (Ribaut, 1923). AM KS 81366, ♀, Mt Koghis. A, ventral view of maxillipede, scale 100μm; B, detail of dental margin of maxillipede coxosternite, scale 50μm; C, ventral part of mandibular gnathal edge, showing aciculae, scale 10μm; D, dorsal view of coxal processes of first maxillae and inner margins of telopodites, scale 20μm; E, cephalic pleurite, showing Tömösváry organ, scale 50μm; F, distal articles of antenna, scale 50μm; G, gonopods, scale 50μm.

Australia (Museum Victoria NOH-1778, 1782, 1786), and the coxosternite shape more closely resembles the adult shape than is the case between the much more similar sized specimens of *E. humilis* and *E. tridentatus*. *Lamyctes fulvicornis* (=*L. emarginatus*) likewise acquires its adult dental formula (2+ pseudoporodont) in LII, and the LII dental margin is similar to that of the mature stages (Andersson, 1984, fig. 6). The substantial differences between the coxosternal shape of *E. humilis* and the smallest specimens of *E. tridentatus* are thus unlikely to be attributable to ontogenetic change in a single species.

A few other differences between small (*E. humilis*) and larger (*E. tridentatus*) specimens are atypical for ontogenetic variation. The holotype of *E. humilis* and two additional specimens assigned to that species have a prominently rounded (convex) median sector to the posterior margin of T7, whereas this sector of the margin is at most weakly convex in *E. tridentatus*. Elaboration of tergal margins is typically enhanced, rather than suppressed, in lithobiomorph ontogeny (e.g., projections become more prominent: Andersson, 1981) so the modified margin of the small specimens appears to have taxonomic significance. The holotype of *E. humilis* and ♀ QM S60637 have a relatively longer antenna than do any specimens of *E. tridentatus*, the elongation deriving from a larger number of articles (maximum 33 in these specimens) and an elongation of the distal articles. The penultimate and adjacent articles in *E. humilis* are longer than wide (Fig. 7F), the reverse of the condition in *E. tridentatus* (Fig. 4D). The ♂ gonopod of the holotype of *E. humilis* (Ribaut, 1923, fig. 26) is more setose than is that of larger specimens of *E. tridentatus* (Fig. 3C).

Easonobius tridentatus (Fig. 4F) has a substantially smaller Tömösváry organ than does *E. humilis* (Fig. 7E). This difference may be size-related because several small Henicopidae have large Tömösváry organs; this is observed repeatedly in blind lineages [Anopsobiinae; *Lamyctes coeculus*; *Paralamyctes* (*Haasiella*) *trailli*] but also in some small species that retain ocelli [*P.* (*Haasiella*) *cammooensis* and *P.* (*H.*) *ginini*].

Modified setae on the coxal process of the first maxilla also serve to distinguish the species. *Easonobius tridentatus* has several lacinate setae near the dorsal margin of the coxal process, above the main cluster of simple setae (Figs. 5I), with branching confined to a few spines at the

distal tip of the setae (Fig. 6H). In *E. humilis*, a single plumose seta (Fig. 7D) is instead present in addition to the simple setae.

Easonobius humilis (Ribaut, 1923)
(Fig. 7)

Paralamyctes humilis: Ribaut, 1923: 23, figs 24-26.
Paralamyctes humilis: Würmli, 1974: 526, fig. 2.
Analamyctes humilis: Chamberlin, 1955: 50.
Analamyctes humilis: Edgecombe, 2001: 206.

DIAGNOSIS. Wide head shield 0.75-0.8mm; penultimate and preceding few antennal articles longer than wide; dental margin of maxillipede coxosternite narrow, with 2+2 teeth, margin strongly sloping posterolaterally distal to outer tooth; Tömösváry organ large; single plumose seta near dorsal edge of coxal process of first maxilla; posteromedian embayment in margin of T7 convex; tergites lacking spinule-like setae.

MATERIAL. HOLOTYPE. Naturhistorisches Museum Basel, Zoologische Abteilung 303a, ♂, Oubatche, Province Nord, New Caledonia. OTHER MATERIAL. New Caledonia, leg. G.B. Monteith. PROVINCE SUD: AM KS 81366, ♀ (Fig. 7A-G), Mt Koghis, 22°11'S 166°01'E, 750m, 29 November 2000; AM KS 82627, ♂, Mt Koghis, 500m, 2-3 November 2002; QM S60637, ♀, S60651, ♀, Mt Humboldt, source, 21°53'S 166°24'E, 1300 m, 5-8 November 2002, rainforest.

DISCUSSION. Specimens from Mt Koghis (Fig. 7) and Mt Humboldt are assigned to *E. humilis* despite the substantial geographic distance from the type locality. The specific diagnosis indicates characters that these specimens share with each other to the exclusion of the larger *E. tridentatus*. The five specimens have a maximum number of 26, 28 (N=2) and 33 (N=2) antennal articles. The strength of tarsal articulations on anterior legs varies between specimens from the same locality (faint on Mt Humboldt specimen QM S60637 as in the holotype; well defined on Mt Humboldt specimen QM S60652). Coxal pore counts are 1,1,2,2/1,1,2,2 (holotype) and 1,2,2,2/0,2,2,2 (AM KS 82627) in males and 1,2,2,2/1,2,2,2 in females. The female gonopods (Fig. 7G) have a pair of bullet-shaped spurs with their bases adjacent to each other (see also Würmli, 1974).

PHYLOGENETIC RELATIONSHIPS

Morphological characters of *Easonobius humilis* and *E. tridentatus* are scored for the character set of Edgecombe (2003b). Several new characters (characters 52-57 in Table 1) bear on the relationships of *Henicops* and *Lamyctopristis*. Other than adding the two New Caledonian species, taxonomic sampling is as in

Edgecombe (2003b) except for the inclusion of *Lamyctopristus* (*Eumyctes*) *sinuatus* (Porat, 1893), as discussed above, and *Paralamyctes* (*Paralamyctes*) *asperulus* Silvestri, 1903 (=*P. tabulinus* Attems, 1928; see Edgecombe, 2003a). This species is included to test Chamberlin's (1955) concept of a New Caledonian/South African clade (his '*Capolamyctes*' concept).

Data were analysed with PAUP* version 4.0b10 (Swofford, 2002). A heuristic search used 5,000 random stepwise addition sequences that sampled five trees per iteration, followed by TBR (tree bisection-reconnection) branch swapping on these trees. Cladograms were rooted with Lithobiidae as outgroup to Henicopidae. Multistate characters were coded as unordered. Node support was evaluated via parsimony jackknifing (Farris et al., 1996). Jackknife frequencies were computed with PAUP* with 1000 replicates having 33% deletion. Each jackknife replicate involved a heuristic search with 20 random stepwise addition replicates and TBR branch swapping on 20 trees per replicate.

With the above analytical procedures, 4,233 shortest cladograms of 135 steps (Consistency Index 0.54; Retention Index 0.82; Rescaled Consistency Index 0.44) were found in all 5,000 replicates. Figure 8 depicts clades resolved in more than half of the jackknife replicates, indicating which of these groups are collapsed in the strict consensus. All clades with more than 50% jackknife support are present in all shortest cladograms.

A *Lamyctes-Henicops* Group is one of the most strongly supported clades in Henicopidae based on molecular data (Edgecombe et al., 2002; Edgecombe & Giribet, 2003b). This group, which includes the nominate genera together with *Analamyctes*, *Easonobius*, *Eumyctes* and *Lamyctopristus*, is supported in 78% of the shortest morphological cladograms, with a
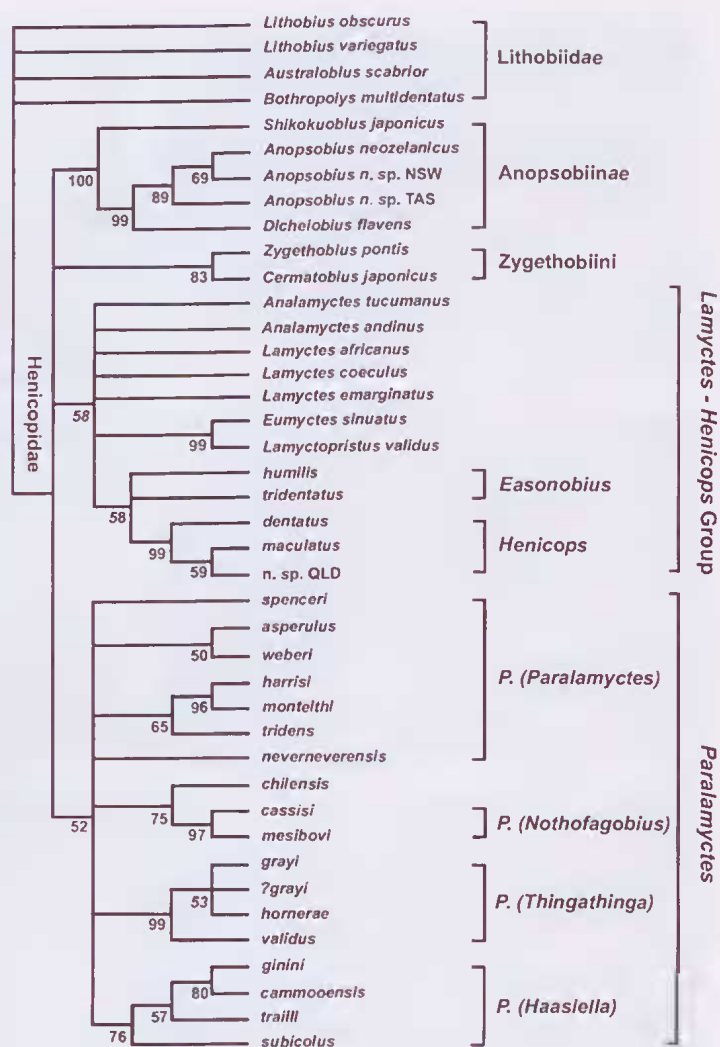

FIG. 8. Consensus of clades present in more than 50% of jackknife replicates based on morphological data in Table 2, showing jackknife frequencies. Groups with jackknife frequencies in italics are contradicted in some of the 4,233 minimal length cladograms.

jackknife frequency of 58%. Apomorphies indicating membership of *Easonobius* in the *Lamyctes-Henicops* Group are the alternation of groups of short and long antennal articles (Fig. 4E) and an abrupt transition in the structure of the fringe of branching bristles on the mandible (characters 4:1 and 25:1, respectively). Within the group, only *Henicops* and a clade that unites *Eumyctes* and *Lamyctopristus* are present in all minimal length cladograms and have strong jackknife support (both 99%); the inter-relationships of species assigned to *Lamyctes*,

TABLE 1. Morphological characters used in phylogenetic analysis (see Edgecombe et al., 2002; Edgecombe, 2003b, for descriptions and discussion of characters 1-51).

1. Ocelli: (0) cluster of ocelli; (1) single ocellus.

2. Convexity of ocellus: (0) bulging; (1) flattened.

3. Antennal segmentation: (0) 17 or more segments; (1) 15 segments.

4. Change in lengths of antennomeres: (0) gradual change in length along antenna; (1) markedly uneven in proximal part of antenna, with short, paired antennomeres interspersed between groups of longer ones.

5. Long, tubular antennomeres: (0) some antennomeres equally wide and long, proximal two antennomeres much larger than succeeding few; (1) all antennomeres longer than wide, proximal two antennomeres not substantially larger than succeeding few.

6. Tömösváry organ: (0) on small sclerotisation anteroventral to ocelli; (1) near margin of cephalic pleurite; (2) near midwidth of cephalic pleurite.

7. Tömösváry organ on margin of head: (0) organ on surface of cephalic pleurite; (1) organ in membranous field on margin of head.

8. Median furrow on head shield: (0) terminates in front of transverse suture; (1) deep and continuous to transverse suture.

9. Shoulder in labral margin: (0) absent; (1) present.

10. Pleurites of maxillipede segment connected ventrally, forming a continuous band between maxillipede coxosternite and sternite of first pedigerous segment: (0) pleurites discontinuous; (1) pleurites continuous.

11. Shape of maxillipede coxosternite: (0) subtriangular coxosternite with narrow, curved dental margin; (1) subtrapezoidal coxosternite with narrow, straight dental margin; (2) narrow dental margin, markedly V-shaped, with deep median notch; (3) subsemicircular coxosternite with wide, convex dental margin; (4) trapezoidal coxosternite with narrow, curved dental margin; (5) wide, subtransverse dental margin; (6) narrow, straight dental margin projected forward; (7) trapezoidal coxosternite with moderately wide, weakly V-shaped dental margin.

12. Paired cusps on teeth on maxillipede coxosternite: (0) absent (unpaired, conical teeth); (1) present.

13. Porodont: (0) absent; (1) translucent, seta-like porodont; (2) conical, tooth-like pseudoporodont.

14. Proportions of maxillipede tarsungulum: (0) pretarsal section of approximately equal length to tarsal section; (1) pretarsal section much longer than tarsal section.

15. Dense setation on inner part of maxillipede tibia and femur: (0) absent; (1) present.

16. Body narrowed across anterior part of trunk: (0) T1 of similar width to head and T3; (1) T1 markedly narrower than head and T3.

17. Angulation (projections) of posterolateral corners of tergites: (0) some angular or toothed; (1) all rounded.

18. Posterior margin of tergite 7 embayed, with median sector straight and thickened ventrally: (0) absent; (1) present.

19. Course of posterior margin of tergite 8: (0) concave; (1) transverse.

20. Spiracle on first pedigerous trunk segment: (0) absent; (1) present.

21. Row of digitiform pinnules with pointed tips along dorsal edge of aciculae: (0) absent; (1) present.

22. Entire acicula series simple: (0) absent; (1) present.

23. Fringe of branching bristles on mandible: (0) extends along entire gnathal margin, skirting aciculae; (1) terminates at aciculae.

24. Ventral bristles in fringe on mandible with a wide base: (0) absent; (1) present.

25. Differentiation of branching bristles on mandible: (0) branching structure of bristles grades evenly along fringe; (1) abrupt transition between rows of scale-like bristles and single row of plumose bristles.

26. Width of fringe of branching bristles dorsally: (0) fringe narrowed dorsally, not developed along all bristles of furry pad; (1) fringe wide, dense, developed along whole length of furry pad.

27. Accessory denticles on mandible all triangular, continuous between teeth, without grooved ridges on teeth: (0) absent; (1) present.

28. Furry pad intergrades with accessory denticles: (0) absent; (1) present.

29. Shape of first maxillary sternite: (0) small, wedge-shaped, with median suture; (1) large, bell-shaped, coxae not merged anterior to sternite, suture between coxa and sternite confined to posterior edge of maxilla.

30. Basal joint of telopodite of first maxilla fused on inner side to coxal process: (0) telopodite distinctly demarcated; (1) telopodite fused to adjacent part of coxa.

31. Setae on coxal process of first maxilla: (0) dense cluster of differentiated setae; (1) simple setae; (2) laciniate setae or plumose amidst simple setae.

32. Coxa of leg 15 with long, lobate process ending in a spine: (0) absent; (1) present.

33. Prefemur of leg 15 with spurs: (0) spurs absent; (1) single ventral spur; (2) several spurs in a whorl.

34. Coxal pores: (0) on legs 14 and 15 only; (1) on legs 13-15 only; (2) on legs 12-15 only; (3) on legs 11-15.

35. Coxal pores set in deep groove, largely concealed by anteroventral face of coxa in ventral view: (0) absent; (1) present.

36. Distal spinose projections on tibiae of legs 1-11: (0) absent; (1) present.

37. Distribution of distal spinose projections on tibiae: (0) strong projection on legs 1-11 only (weak projection variably distinct on leg 12); (1) strong projection on legs 1-12 only; (2) strong projection on legs 1-13 only; (3) strong projection on legs 1-14 only; (4) strong projection on legs 1-15.

38. Tarsus of legs 1-12: (0) divided into basitarsus and distitarsus; (1) undivided.

39. Articulation between basitarsus and distitarsus on anterior pairs of legs: (0) distinct on dorsal side of leg; (1) fused on dorsal side of leg, distinct ventrally.

40. Subdivision of basitarsus indicated by paired larger setae: (0) absent; (1) present.

41. First tarsal segment of legs 1-12 bisegmented (tripartite tarsus): (0) absent; (1) present.

42. Accessory apical claws: (0) anterior and posterior accessory claws; (1) posterior accessory claw only. Supposed absence of an anterior accessory claw in Lamyctopristus validus (Edgecombe, 2003b) is in error. A leg associated with the holotype has an anterior and posterior accessory claw.

43. First genital sternite of ♂ divided longitudinally into two sclerites: (0) undivided; (1) divided.

44. Segmentation of ♂ gonopod: (0) four segments with a seta-like terminal process; (1) stout gonopod with one or two segments.

45. Number of spurs on ♀ gonopod: (0) two; (1) three; (2) five to seven.

46. First article of ♀ gonopod extended as a short process: (0) absent; (1) present.

47. Claw of ♀ gonopod: (0) simple (unipartite); (1) tripartite, dorsal and ventral accessory denticles present.

48. Tömösváry organ large, positioned posteriorly on pleurite: (0) absent; (1) present.

49. Maxillipede teeth progressively decreasing in size and spacing medially: (0) absent; (1) present.

50. Aciculae differentiated into two (outer and inner) rows: (0) absent (single row of aciculae); (1) present.

51. Accessory denticles on dorsal part of mandible: (0) simple, triangular accessory denticles; (1) flattened, multifurcating scales; (2) tuberculate scales.

52. Tergal tuberculation: (0) absent or faint; (1) strong, more pronounced in ♂♂ than ♀♀.

53. Distitarsus of leg 15 divided: (0) undivided (single tarsomere); (1) divided into two or more tarsomeres.

54. Curvature of distitarsal part of leg: (0) straight; (1) curved.

55. Insertion of anterior pretarsal accessory claw: (0) on dorsolateral side of main claw; (1) on ventrolateral side of main claw. Most henicopids have the anterior and posterior accessory claws originating dorsolaterally on the main claw (Fig. 5I1 for Easonobius tridentatus; Fig. 1G for Henicops maculatus). Some species of Paralamyctes (Paralamyctes) (Fig. 1H) and Eumyctes sinuatus (Fig. 1F) have the anterior accessory claw originating near the ventral margin of the main claw.

56. Definition of scutes on pretarsal accessory claws: (0) absent or weak; (1) strong (Edgecombe & Giribet, 2003a: character 57).

57. Definition of scutes on proximodorsal part of main pretarsal claw: (0) distinct; (1) indistinct (Edgecombe & Giribet, 2003a: character 58).

TABLE 2. Codings for 57 morphological characters listed in Table 1.

Lithobius obscurus	0-0000-000 0011000000 0000000000 002200-000 0101001000 0000-00
Lithobius variegatus rubriceps	0-0000-000 7011000000 0000000000 002200-000 0101000000 0000-00
Australobius scabriar	0-0000-000 7010000000 0000000000 002200-000 0101101000 0000-00
Bothropolys multidentatus	0-0010-000 2011000000 0000000000 002200-000 0101001000 0000-00
Shikakuobius japonicus	--00010001 0010001010 0010010000 11120101-0 0000000000 2000000
Dichelabius flavens	--00010101 2010001010 0010010000 11100101-0 0000010000 2000001
Anopsobius neozelanicus	--10010101 2110001000 0010010000 11100111-0 0000010000 2000001
Anopsohius sp. nov. NSW	--10010101 2110001010 0010010000 11100111-0 0000010000 2000001
Anopsobius sp. nov. TAS	--10010101 2010001010 0010010000 11100111-0 0000010000 2000001
Zygethobius pontis	1000010001 3000000100 0010010101 1003113000 0000000000 0000000
Cermatobius japonicus	1100010001 3001000100 0000010111 10021120?0 0000100000 0011000
Lamyctes emarginatus	1001010001 0020001001 0001000001 10020101-0 0000000000 1000000
Lamyctes africanus	1001010001 0020001001 0001000001 10020111-0 0010000000 1000000
Lamyctes caeculus	--00010001 0020001001 0001000001 10020101-0 00??000100 1000000
Lamyctapristus validus	1001010001 0021000001 000??00001 10020131-0 0000200001 ?1011??
Lamyctopristus (Eumyctes) sinuatus	1001010001 0001000001 0001000001 10020131-0 0000000001 0101100
Henicops maculatus	1001020001 1000000001 0001000001 2002013011 1010000001 0010000
Henicops dentatus	1000010001 1000000101 0001000001 2002013011 1010000001 0010000
Henicops sp. nov. QLD	1001020001 1000000001 0001000001 2002013011 0010000001 0010000
Analamyctes tucumanus	1001010001 0000001001 0001000001 1002012000 0000000000 0000000
Analamyctes andinus	1001010001 0020001001 0001000001 1002013000 0000000000 1000000
Paralamyctes (Paralamyctes) spenceri	1000010101 4001000001 1000000111 1002012000 0000000000 0000000
Paralamyctes (Paralamyctes) asperulus	1000010101 4001000101 1000000111 1002012000 0000000000 0000100
Paralamyctes (Paralamyctes) weberi	1000010101 4001000001 1000000111 1002013000 0000000000 0000100
Paralamyctes (Paralamyctes) tridens	1000011101 3001000001 1000000111 1002012000 0000000000 0000000
Paralamyctes (Paralamyctes) manteithi	1000111111 3001100001 1000000111 1002013000 0000000000 0000100
Paralamyctes (Paralamyctes) harrisi	1000111111 3001100001 1000000111 1002013000 0000000000 0000000
Paralamyctes (Paralamyctes) neverneverensis	1000010101 4000000001 1000000111 1002014000 0000000000 0000000
Paralamyctes chilensis	1000010101 4000010001 0000000011 1002013000 0000010000 0000000
Paralamyctes (Nothofagobius) cassisi	1000010101 4000010001 0100001011 1002014000 0000110000 0000000
Paralamyctes (Nothofagobius) mesibovi	1000010101 4000010001 0100001011 1002014000 0000110000 0000000
Paralamyctes (Thingathinga) grayi	1100010111 5001000101 0100000011 1002113010 0000000000 0000011
Paralamyctes (Thingathinga) ?grayi	1100010111 5001000101 0100000011 1002014010 0000000000 0000011
Paralamyctes (Thingathinga) hornerae	1100010111 5001000101 0100000011 10?201?010 0000000000 0000011
Paralamyctes (Thingathinga) validus	1000010111 5001000001 0100100011 1002114010 0000000000 0000011
Paralamyctes (Haasiella) trailli	--00010101 6001000011 0000000011 10020121-0 0000000110 0000000
Paralamyctes (Haasiella) subicolus	1100010101 5001000011 0000000011 10020131-0 0000000010 0000000
Paralamyctes (Haasiella) cammooensis	1100010101 4000001011 0000000011 10020111-0 0000000110 0000000
Paralamyctes (Haasiella) ginini	1100010101 4000001011 0000000011 10020111-0 0000000100 0000000
Easonobius humilis	1001010001 0000000101 0001000001 20?2012000 0000000000 00?0000
Easonobius tridentatus	1001010001 1000000101 0001000001 2002012000 0000000000 0000000

Analamyctes and *Easonobius* are labile. Amongst the minimal length cladograms, the two species assigned to *Easonobius* have three alternative resolutions: monophyletic sister group of *Henicops*, monophyletic sister group of *Analamyctes tucumanus*, or paraphyletic with *E. tridentatus* being closer to *Henicops* than is *E. humilis*.

Parsimony jackknifing favours a closer relationship between *Easonobius* and *Henicops* than with *Analamyctes*, the former grouping having a jackknife frequency of 58%.

Easonobius tridentatus in particular shares its shape of the maxillipede coxosternite (character 11:1) with *Henicops*, closely resembling species such as *Henicops dentatus* in having a gently convex dental margin with the outermost (third) tooth set well inward of the anterolateral corner (Fig. 5A, B). The coxosternal shape in *E. humilis* (Fig. 7A) is instead more similar to that of *Analamyctes*, *Lamyctopristus* and *Lamyctes* (character 11:0), and in some shortest cladograms the similarity between *E. tridentatus* and *Henicops* is a synapomorphy. A cluster of lacinate setae amidst the simple setae on the coxal process of the first maxilla (character 31:2) is also shared by *Easonobius* (Fig. 6H) and all species of *Henicops*. A similarly positioned group of three laciniate setae was described by Ribaut (1923, and Ribaut's unpublished drawings of the holotype) in another New Caledonian species, *Lamyctes brevilabiatus* Ribaut, 1923. Molecular sequence data suggest that '*Lamyctes*' *brevilabiatus* is nested within *Henicops* as the latter is traditionally delimited (Edgecombe & Giribet, 2003b). This species is excluded from *Easonobius* based on its indistinctly jointed tarsi on legs 1-12, unprojected tergites (e.g., transverse posterior margins of TT11 and 13), and bipartite first genital sternite in the male. It is further distinguished at the species level from both known members of *Easonobius* by its more segmented antenna (38-47 articles in QM S60636, S60651, AM KS 82580, KS 82626) and extreme proximity of the inner two teeth on the maxillipede coxosternite (distance between outer and middle teeth about 2.5 times that between middle and inner tooth).

Alternative relationships for *Henicops* are favoured in some of the shortest cladograms. In particular, *Henicops* and *Lamyctopristus* (including *Eumyctes*) sometimes unite to the exclusion of *Easonobius*, with this resolution being supported by a distal spinose projection on the tibia of leg 14 (character 37:3) and mandibular aciculae differentiated into two rows (character 50:1).

Turning to Chamberlin's (1955) hypothesis that *Easonobius humilis* is especially closely related to South African species, an exemplar of the latter group, *Paralamyctes asperulus*, nests in a monophyletic *Paralamyctes* and, in most minimal length cladograms, in *P. (Paralamyctes)*. That clade is defined by two unique mandibular characters (characters 21:1 and 28:1) as well as molecular synapomorphies (Edgecombe et al., 2002; Edgecombe & Giribet, 2003a). The

classification of this and allied South African *Paralamyctes* with *Easonobius humilis* based on a single, highly homoplastic antennal character (Chamberlin, 1955), is emphatically rejected. The classification of Ribaut (1923), in which *E. humilis* was assigned to *Paralamyctes* based on its bipartite tarsi on all legs (character 38:0), is opposed by the absence of a complete median furrow on the head shield (character 8:0; Fig. 4A) and a reduced, rather than bell-shaped, first maxillary sternite (character 29:0; Fig. 6F). The apomorphic homologues unite *Paralamyctes* (Edgecombe, 2001).

ACKNOWLEDGEMENTS

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NOTE ADDED IN PROOF

Anopsobius n. sp. NSW (Fig. 8, Table 2) has been formalised as *Anopsobius wrighti* Edgecombe, 2003e.